



Voracious invader or benign feline? A review of the environmental biology of European catfish *Silurus glanis* in its native and introduced ranges*

Gordon H Copp^{1,2}, J Robert Britton², Julien Cucherousset^{2,3}, Emili García-Berthou⁴, Ruth Kirk⁵, Edmund Peeler⁶ & Saulius Stakėnas⁷

¹Salmon & Freshwater Fisheries Team, Centre for Environment, Fisheries & Aquaculture Science, Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK; ²Centre for Conservation Ecology, School of Conservation Sciences, Bournemouth University, Fern Barrow, Poole, Dorset, BH12 5BB, UK; ³EcoLab Laboratoire d'Écologie Fonctionnelle, UMR 5245 (CNRS-UPS-INPT), Université Paul Sabatier, Bât. 4R3, 118, route de Narbonne, F-31062 Toulouse, Cedex 9, France; ⁴Institute of Aquatic Ecology, University of Girona, E-17071 Girona, Spain; ⁵School of Life Sciences, Kingston University, Penrhyn Road, Kingston upon Thames, Surrey KT1 2EE, UK; ⁶Centre for Environment, Fisheries and Aquaculture Science, Weymouth, Dorset DT4 8UB, UK; ⁷Department of Freshwater Ecology, Institute of Ecology of Vilnius University, Akademijos 2, LT-08412, Vilnius, Lithuania

Abstract

A popular species for food and sport, the European catfish (*Silurus glanis*) is well-studied in its native range, but little studied in its introduced range. *Silurus glanis* is the largest-bodied freshwater fish of Europe and is historically known to take a wide range of food items including human remains. As a result of its piscivorous diet, *S. glanis* is assumed to be an invasive fish species presenting a risk to native species and ecosystems. To assess the potential risks of *S. glanis* introductions, published and 'grey' literature on the species' environmental biology (but not aquaculture) was extensively reviewed. *Silurus glanis* appears well adapted to, and sufficiently robust for, translocation and introduction outside its native range. A nest-guarding species, *S. glanis* is long-lived, rather sedentary and produces relatively fewer eggs per body mass than many fish species. It appears to establish relatively easily, although more so in warmer (i.e. Mediterranean) than in northern countries (e.g. Belgium, UK). Telemetry data suggest that dispersal is linked to flooding/spates and human translocation of the species. Potential impacts in its introduced European range include disease transmission, hybridization (in Greece with native endemic Aristotle's catfish [*Silurus aristotelis*]), predation on native species and possibly the modification of food web structure in some regions. However, *S. glanis* has also been reported (France, Spain, Turkmenistan) to prey intensively on other non-native species and in its native Germany to be a poor biomanipulation tool for top-down predation of zooplanktivorous fishes. As such, *S. glanis* is unlikely to exert trophic pressure on native fishes except in circumstances where other human impacts are already in force. In summary, virtually all aspects of the environmental biology of introduced *S. glanis* require further study to determine the potential risks of its introduction to novel environments.

Keywords Diet, distribution, environmental impact, growth, habitat use, reproduction

Correspondence:

Gordon H Copp,
Salmon & Freshwater
Fisheries Team, Cen-
tre for Environment,
Fisheries & Aquacul-
ture Science, Pakefield
Road, Lowestoft, Suf-
folk NR33 0HT, UK
Tel.: +44 01502
527751
Fax: +44 01502
513865
E-mail: gordon.copp@
cefasc.co.uk

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Introduction

Non-native fish introductions have a long history in Europe (Copp *et al.* 2005a) and one of the most popular of the successful introductions has been that of the European catfish (*Silurus glanis*, Siluridae). The largest freshwater fish species indigenous to the European continent, *S. glanis* is native to Eastern Europe and western Asia (Kinzelbach 1992), but is now established in at least seven countries to the west and south of its native range (Elvira 2001). *S. glanis*, which is among the 20 largest freshwater fish species worldwide (Stone 2007), is particularly popular amongst European anglers and the species has been the subject of numerous studies related to its increasing use in aquaculture. However, relatively few studies have

been published on the environmental biology of introduced *S. glanis* populations and even less information is available on the species' impact on native biota and ecosystems in its introduced European range. This is perhaps not surprising for countries where *S. glanis* has been introduced in recent decades (e.g. Spain), but it is remarkable for other European locations such as the United Kingdom, where there is only limited data in scientific publications in reference to its general distribution (Hickley and Chare 2004), growth and angler recapture rates (Britton *et al.* 2007) and low abundance in the River Thames (Kirk *et al.* 2002; Copp *et al.* 2007). In light of this paucity of information, the aim of the present paper was to review the published (peer and grey) literature on the environmental biology of *S. glanis* in its native

and introduced European range as a surrogate means of assessing the species potential risk to native species and ecosystems in those parts of Europe where the species is not native (i.e. absent since the last glaciation). This review encompasses all aspects of the species' morphology, distribution, habitat use, migratory behaviour, diet, growth, diseases, and reproduction under natural conditions and, as such, excludes all papers dealing with the aquaculture of *S. glanis* unless they have a direct bearing on the species' environmental biology. The review is concluded with a general discussion on the species' potential invasiveness and consequential threat to native species and ecosystems.

Description and morphology

General description

Silurus is the only existing genus in Europe of the Siluridae family (Ferraris 2007), with the other genera confined to Central and South-East Asia (Berg 1949; Maitland and Campbell 1992; Teugels 1996). There are 18 *Silurus* species of which two are native to Europe: Aristotle's catfish (*Silurus aristotelis*, Siluridae) is endemic to Greece (Phillips and Rix 1988) and *S. glanis* is native to mainland Europe, east of the River Rhine (Fig. 1). However, *S. glanis* has been introduced into a number of countries in Western Europe, such as the UK in the 19th century (Lever 1977) and Spain in the 20th century (Elvira and Almodóvar 2001; Schlumberger *et al.* 2001), and re-introduced after a long absence to previously native distributions in parts of Belgium, the Netherlands and France (Van Neer and Ervynck 1993; Volz 1994). *S. glanis* is an economically important species in commercial and

recreational fisheries as well as in aquaculture (Berg 1949; Adámek *et al.* 1999). The species is a sport fish in some countries (e.g. France, Italy, Spain, UK) and considered a delicacy in others (e.g. Hungary, Poland, Slovakia, Lithuania), where it is exploited for its flesh (tender white meat), skin (for leather and glue production) and eggs (for caviar). The economic importance of *S. glanis* in many central and eastern European countries has increased because the species possesses many characteristics desirable for profitable aquaculture (Proteau *et al.* 1993; Paschos *et al.* 2004) leading to a proliferation of scientific articles on its reproduction, genome manipulation and management (Schlumberger *et al.* 1995; Adámek *et al.* 1999; Triantafyllidis *et al.* 2002; Alp *et al.* 2004). In 1993, estimates of aquaculture production of *S. glanis* in Europe (excluding the former USSR) range from 358 tonnes (Haffray *et al.* 1998) to 602 tonnes (for 10 European countries; Linhart *et al.* 2002) in 1993, rising in 2002 to about 2000 tonnes (Linhart *et al.* 2002) and research on husbandry of the species continues (Paschos *et al.* 2004; David 2006).

S. glanis has an elongated body that is laterally decompressed behind its broad head, which accounts for about 20% of the entire body length and has a rounded, flattened snout and widely-spaced nostrils anterior to the olfactory cavities (Mihálik 1995). *S. glanis* has a triangular-shaped head (Černý 1988) with small eyes and a large mouth, with two very long, slender, flexible cartilaginous barbs on the upper jaw (up to 41.2% of TL; Mukhamediyeva and Sal'nikov 1980) and four short, flexible barbs, which protrude below the lower jaw (Davies *et al.* 2004). These reach as far as the base of the pectoral fins and are, on average, 11.4% of the fish's TL (Mihálik 1995), although in

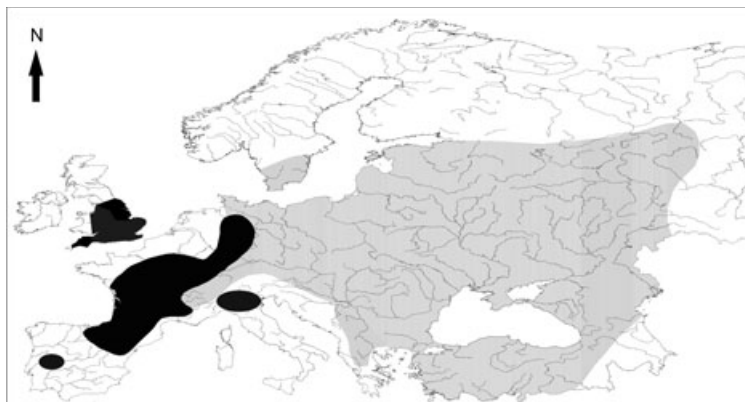


Figure 1 Native (■) and introduced (■) distributional ranges of *S. glanis*. Adapted from Greenhalgh (1999) and updated with information from Rossi *et al.* (1991), Economidis *et al.* (2000), Doadrio (2001), Keith and Allardi (2001), Davies *et al.* (2004) and Kottelat and Freyhof (2007).

some areas ranging 5.3–12.4% of TL (Mukhamediyeva and Sal'nikov 1980). Pigmentation varies according to habitat, but *S. glanis* is generally dark along its back with marbled sides, with a greyish-white belly. Albinism has been reported (Dingerkus *et al.* 1991). The skin is scale-less, coated in mucus, contains sensory cells and contributes to respiration through oxygen absorption and carbon dioxide secretion (Mihálik 1955; Davies *et al.* 2004). Indeed, *S. glanis* at rest is able to withstand prolonged periods of hypoxia depending on water temperature (Massabuau and Forgue 1995).

The dimensions and position of fins on *S. glanis* indicate that the species lives predominantly on the bottom (Mihálik 1995). The powerful pair of pectoral fins (18 rays) sit directly behind the gill covers to the base of the ventral fins. The ventral fins have one hard ray and 12 to 17 soft rays (Mukhamediyeva and Sal'nikov 1980). The pelvic fins are much smaller, situated near the anal opening and contain 10 to 13 soft rays (Mukhamediyeva and Sal'nikov 1980). The anal fin is the longest, being on average 58% of TL, and it stretches from the anal opening to the caudal fin. The anal fin has 90–92 soft rays and 73–106 sturdy rays (Mukhamediyeva and Sal'nikov 1980) extending for about half of the fish's TL. The caudal fin is not very big, rounded and appears cut off at the end and contains 17 to 19 soft rays. On the back, there is no adipose fin and there is only the very small dorsal fin (3–5 rays), which sits at the end of the first third of the body. The first ray of this fin is hard, the other four are soft (Maitland and Campbell 1992; Greenhalgh 1999; Davies *et al.* 2004).

Morphology (relative growth)

There does not appear to be sexual dimorphism in *S. glanis* with regard to any meristic or mensural character other than maximum body depth and girth. Mihálik (1995) reports that the relative length of head, body and tail are in the ratio 5:7:8 and the height of the head ranges from 16.8 to 19.6% of TL; however, the reported range in the Khauz Khan Reservoir (Turkmenistan) is 8.8–14.1% of TL (Mukhamediyeva and Sal'nikov 1980). Considerable variability in body and head characters was observed at the onset of piscivory (Lysenko 1978) and this emphasizes the size and age variability in *S. glanis* morphology. When comparing groups I (5–23 cm) and II (24–49 cm), Lysenko (1978) observed differences in 75% of the morpho-

logical characters examined. These included size-dependent increases in the proportions of some characters (body depth, pecto-ventral and pre-anal distances, anal fin length and height, head and dentary lengths) and decreases in others (head depth, eye diameter, pre-dorsal and post-dorsal distances). Shifts in body and head proportions were noted in *S. glanis* 36–67 cm TL, i.e. prior to attainment of sexual maturity, but became less apparent in larger fish (>135 cm TL). The least variable characters were body depth and base length of dorsal fin.

There is also some geographical variability in morphology reported in *S. glanis*, with differences in the meristic characters of *S. glanis* after the species introduction to Lake Balkhash relative to *S. glanis* in other waters and, in particular, the parental stock from the River Ural (Lysenko 1978). The differences between the Balkhash and Ural *S. glanis* were with respect to 6 of the 21 characters compared, whereby the introduced Balkhash fish had smaller proportional values for some characters (head depth, inter-orbital distance, maximum body depth, dorsal-fin base length) and greater values for other characters (anal fin length, number of gill rakers on the first arch). These differences were considered to be adaptations to the different diet and environmental conditions *S. glanis* encountered in Lake Balkhash relative to those in the River Ural (Lysenko 1978).

Distribution and habitat

Native distribution

S. glanis is a Eurasian species that originally evolved in Asia before subsequently expanding its range to the west (Bornbusch 1995). Migration into the European rivers Danube, Dnieper and Volga was via the Caspian, Black and Aral seas (Lever 1977) and facilitated by the relatively low salinity levels (up to 15 ‰) along the coastal areas, for *S. glanis* is not particularly saline tolerant (Udrea 1977; Linhart and Billard 1992; Stolyarov and Abusheva 1997). Their native distribution extends from Germany eastwards through to Poland, up to Southern Sweden and down to Southern Turkey and north Iran stretching through the Baltic States to Russia (Greenhalgh 1999) and to the Aral Sea of Kazakhstan and Uzbekistan (Phillips and Rix 1988). Genetic analyses have revealed that, within this natural distribution, there is a lack of geo-

graphic sub-structuring and differentiation between populations (Krieg *et al.* 2000), which results from the paleogeography and hydrographics of the basins concerned. As many of these basins were tributaries of seas that were interconnected at the end of the last glacial period, migration and gene flow between populations was possible until relatively recently (when salinity levels increased), preventing the development of substantial genetic differentiation (Bianco 1990; Krieg *et al.* 2000).

Within its natural range, threats to *S. glanis* populations include climate, habitat and species introductions. For example, *S. glanis* populations in Sweden are reported to be at acute risk from climatic changes that have occurred since the species' natural migration and establishment in that area (Nathanson 1987); this threat is compounded by a shortage of suitable environments for the species in southern areas of the country (Nathanson 1995). In Greece, *S. glanis* is native to certain lakes into which numerous species have been introduced or transferred. For example, *S. aristotelis*, which in Greece is endemic to the River Acheloos catchment only, was introduced to Lake Volvi where it is said to have out-competed the native *S. glanis*, leading to its extinction (Economidis *et al.* 2000).

Non-native distribution

S. glanis has been introduced to at least seven different European countries (Fig. 1) and has successfully established self-sustaining populations up to six of these (Elvira 2001), although confirmed, self-sustaining reproduction is lacking for at least half this number. *S. glanis* is said to have been extirpated from two European countries (i.e. Denmark, Finland; Froese and Pauly 2007), although other authors suggest it is still present in Denmark (Elvira 2001; DK Zoologisk Museum og Danmarks Fiskeriundersøgelse 2007). Introductions of *S. glanis* to neighbouring countries of Europe include Algeria and Tunisia (Froese and Pauly 2007).

The introduction of *S. glanis* to the British Isles is a particular case, because of its geographical separation from mainland Europe. *S. glanis* was first introduced in 1880 into two lakes at Woburn Abbey, Bedfordshire (Lever 1977; Davies *et al.* 2004), from which natural dispersal was not possible (Wheeler 1974). The Woburn stock was then used to establish *S. glanis* in other waters nearby (Phillips and Rix 1988), with *S. glanis*

currently inhabiting >250 water bodies (Clarke 2005). Although *S. glanis* has been introduced to water bodies across the UK (Fraser 1979), concentrations are found in the South East and Midlands (Clarke 2005). Seemingly capable of spawning in England (Fraser 1979), success appears constrained by relatively low-water temperatures (David 2006) and its range remains limited. Until recently, *S. glanis* was rarely observed in large rivers (Kirk *et al.* 2002) and there is no evidence yet of the species establishing a self-sustaining population in any UK river system of suitable size (Wheeler 1974; Copp *et al.* 2007).

Introductions of *S. glanis* throughout Europe have been for both aquaculture and angling (Copp *et al.* 2005a), with the species becoming increasingly popular with anglers throughout Europe because of their large size and relatively frequent capture. For example, the introduction of *S. glanis* to Italy in the early 20th century was for aquaculture, but the species was also introduced to the ponds of private fishing reserves (Gandolfi and Giannini 1979; Boldrin and Rallo 1980) and subsequently reported in rivers from the 1930s onwards (Gandolfi and Giannini 1979; Boldrin and Rallo 1980). Indeed, there has been a proliferation in the number of still waters containing *S. glanis* in the last 20–30 years (Copp *et al.* 2005a). And although introductions of non-native species such as *S. glanis* are theoretically regulated by legislation in most European countries (Copp *et al.* 2005a), the proliferation of waters hosting the species has been assisted by unregulated introductions in many countries (Boldrin and Rallo 1980; Inskipp 2003; Hickey and Chare 2004; Clavero and García-Berthou 2006).

Another reason for *S. glanis* introductions has been as a biocontrol agent for regulating cyprinid fish numbers. This introduction of *S. glanis* to the Netherlands (from Hungary) resulted in their accidental escape and dispersal to other waters (Boeseman 1975). A similar pattern of introduction by escape was reported for Belgium and France, where *S. glanis* was apparently 'introduced' from Eastern Europe in 1857 for aquaculture. However, subsequent archaeological evidence demonstrated that *S. glanis* was originally native to parts of Belgium, the Netherlands and France (Van Neer and Eryvynck 1993; Volz 1994). The species apparently disappeared from all three of these countries for a period of time (Bruylants *et al.* 1989; De Nie 1996 in Simoens *et al.* 2002; Louette *et al.* 2002), but has been re-categorized as 'reintroduced' to

Flanders (Verreycken *et al.* 2007) and the Rhône valley in France (Valadou 2007). Other *S. glanis* have entered the Netherlands from neighbouring countries, as escapee fish upstream of aquaculture facilities (in Germany) that migrated naturally down the River Rhine (De Groot 1985).

Wild populations of re-introduced *S. glanis* have done quite well in France, especially in the south-west (Valadou 2007) and in the River Saône (DIREN Rhône-Alpes 2004) – the latter a consequence of *S. glanis* escapes into the River Doubs in about 1890 (Valadou 2007). However, the species occurs in limited numbers in the Flemish part of Belgium and is probably reproducing (Simoens *et al.* 2002). Activities at Lake Schulen in Flanders reveal how re-introduced populations can establish following an introduction. This shallow, man-made lake was built as a flood storage reservoir, with extensive fish stock assessments completed in 1988 (no *S. glanis*) and 1999 (*S. glanis* were found). It transpired that a number of large individuals, which been illegally introduced by anglers in the early 1990s, had successfully reproduced culminating in the capture of eight juveniles (8–14 cm) in the 1999 survey (Simoens *et al.* 2002). The introduction of *S. glanis* into rivers in countries such as Spain has resulted in the establishment of abundant populations in at least four river basins (Elvira and Almodóvar 2001; Benejam *et al.* 2007; Carol *et al.* 2007a), with recreational anglers now catching individuals to >75 kg.

Habitat use

The species is normally encountered throughout their range in large rivers, lakes and coastal areas of low salinity (<15 ‰). Primarily a fish of rich, weedy lakes and slow, deep lowland rivers, in its native range, the species is known to shift during their first year of life into mid channel habitats (Wolter and Vilcinskis 1996; Wolter and Freyhof 2004), which are important for reproduction and habitat partitioning between different age groups (Wolter and Bischoff 2001). However, the preferred habitat of *S. glanis* is still waters (Wheeler 1969; Greenhalgh 1999). During winter, it hibernates in rivers in deep holes, dens and crevices in the bed; in lakes, it lies in the lower third of the water column or on soft mud (Lelek *et al.* 1964; Lelek 1987). The species does not have high oxygen requirements (Lelek 1987); because its blood contains 30–35% haemoglobin, it can use small amounts of oxygen efficiently, with

its tolerance limit being around 3.0–3.5 mg L⁻¹ (Mihálik 1995). This also makes it relatively tolerant of pollution (Lelek 1987). Its geographic distribution reveals it is capable of surviving under different climates and water temperature regimes, indicating a tolerance of relatively low temperatures (Hilge 1985), although the species' physiological optimum is 25–27 °C and lower temperatures may inhibit the expression of certain biological traits, such as somatic growth (David 2006; Britton *et al.* 2007).

Telemetry studies have revealed that habitat use follows a diurnal pattern, incorporates strong site fidelity and/or territorial behaviour (Carol *et al.* 2007b). There is intensive daytime use of littoral habitat, with resting places within dense vegetation or in areas over-grown with bulrushes and tree roots (Abdullayev *et al.* 1978; Bruton 1996; Carol *et al.* 2007a, 2007b). Activity peaks during the night, with movements both within and outside of the normal resting places. These are motivated by hunger stimuli and movements follow the paths of their prey (Pohlmann *et al.* 2001; Carol *et al.* 2007a, 2007b). This nocturnal foraging is assisted by the species' well-developed non-visual sensors and organs (Bruton 1996). In a Czech river, activity was low in spring and winter with the peaks during daylight, in autumn, maximal movement was recorded during dusk, whereas in summer *S. glanis* were active across the whole 24 h (Slavík *et al.* 2007). Movement was inversely related to flow rate, except in summer, when maximal home ranges occurred, being larger for adults. Juveniles and adults were spatially segregated, except when water flow increased (Slavík *et al.* 2007).

Natural diet

Senses and detection of prey

In addition to the oral cavity, *S. glanis* also possesses taste organs elsewhere on its body surface (e.g. lips, barbels, fins and skin of head and body), with receptors of sweet, sour, bitter and salt tastes (Malyukina and Martem'yanov 1981). *S. glanis* has large olfactory and supplementary sacs, with a considerable area of receptor surface because of numerous folds of the olfactory rosette (Devitsina and Malyukina 1977). The detection of food items is based predominately on this sense (Mihálik 1995). *S. glanis* also possesses an electroreceptive system, which may well function in prey detection

(Bretschneider 1974) as well as hearing that is exceptionally sensitive to extra-aquatic sounds – this is thought to be because the relatively immobile vertebrae attached to the head have grown together to form the Weber's apparatus (Mihálik 1995). This connects the hearing organ in the skull to the swim bladder producing an effective sound amplifier (Maitland and Campbell 1992). With its well-developed non-visual sensors, *S. glanis* is well adapted to living in fresh waters with low visibility and consequently has small eyes and restricted vision (Bruton 1996). The species makes use of its feelers and taste organs, which include fleshy lips, protruding lower jaw (which supports four inflexible short barbels) and upper jaw, which has two long, flexible, cartilaginous barbels (Mihálik 1995). The barbels of *S. glanis* are also highly developed in smell detection and therefore the species can follow prey by the chemicals they produce, with the 'odour' of a stressed prey fish acting strongly on the predator (Malyukina and Martem'yanov 1981). As such, *S. glanis* are guided by the hydrodynamic and chemical traces in wakes that follow swimming fishes, such as is evident in the species ability to track accurately the three-dimensional swim path of prey before an attack in complete darkness (Pohlmann *et al.* 2001). Owing to its highly developed sense of taste and smell, its reliance on sight is reduced, enabling it to feed at night and location of prey, with no problems in orientation during complete darkness (Malyukina and Martem'yanov 1981; Pohlmann *et al.* 2001). Consequently, this species has a strong nocturnal feeding activity (Boujard 1995) and feeding usually takes place 1 h after dusk until just before dawn (Anthouard *et al.* 1987).

Prey selectivity or preference

S. glanis is considered to be an opportunistic, omnivorous forager and its diet often cuts across the spectrum of the ichthyofauna in its habitat reflecting the available species (Stolyarov 1985). Although the diet composition of *S. glanis* changes slightly with age, the predominant prey type normally reflects the most abundant fish species of suitable size and habitat use (Omarov and Popova 1985). This is apparent in the example of *S. glanis* in the Khauz-Khanskoye Reservoir (Turkey), where common carp (*Cyprinus carpio*, Cyprinidae), goldfish (*Carassius auratus*, Cyprinidae), roach (*Rutilus rutilus*, Cyprinidae) and sharpbelly (*Hemiculter leucisculus*, Cyprinidae) were the main prey in 1971, but by

1975, *R. rutilus* was declining in importance and the non-native *H. leucisculus* had become the predominant prey (Mukhamediyeva and Sal'nikov 1980).

The dietary spectrum of *S. glanis* is greater than, for example, northern pike (*Esox lucius*, Esoxidae) or pikeperch (*Sander lucioperca*, Percidae) and thus may be able to exploit the breadth of available food more comprehensively and more completely (Bekbergenov and Sagitov 1984; Mihálik 1995). However, unlike the two former species, *S. glanis* has not been found to exert the same 'top-down' influence on lacustrine food webs (Wysujack and Mehner 2005), in direct contrast to suggestions elsewhere (Raaf 1990; Adámek *et al.* 1999) that *S. glanis* could be used as a bio-manipulation tool to control cyprinids. Reasons behind the large diet spectrum in *S. glanis* may lead to questions about its efficiency as a predator or the degree of selectivity for prey. The choice of prey may be related to its density, its defence abilities or the particular preferences of *S. glanis*. Under controlled experimental conditions, 1-year-old *S. glanis* have been observed to avoid (i.e. take less often than expected) certain species such as roach, chub (*Leuciscus cephalus*, Cyprinidae), topmouth gudgeon (*Pseudorasbora parva*, Cyprinidae) and gibel carp (*Carassius gibelio*, Cyprinidae) (Adámek *et al.* 1999), the latter two of which are not native to *S. glanis* diet. However, the apparent avoidance of these species (Adámek *et al.* 1999) should be considered with caution, given that: (i) at least some of the species (e.g. *R. rutilus*) are very commonly found in the diet of wild *S. glanis* (Table 1); (ii) the experiments were with < 6 specimens of *S. glanis*, two of which were albino fish meaning that they were of domesticated, ornamental origin; and (iii) no strong preferences for any fish species were found in the experiments with Ivlev electivity values being <0.19 on a scale from -1.0 to +1.0. Conversely, preferences have been reported for asp (*Aspius aspius*, Cyprinidae), sunbleak (*Leucaspis delineatus*, Cyprinidae), rudd (*Scardinius erythrophthalmus*, Cyprinidae) and bitterling (*Rhodeus amarus*, Cyprinidae) and prey body shape is not thought to be a factor influencing prey preference (Adámek *et al.* 1999). A common feature in the natural diet of *S. glanis* (Omarov and Popova 1985; Pouyet 1987; Wysujack and Mehner 2005) is the positive relationship between predator size or age and prey size (Fig. 2), although they eat relatively smaller fish than other piscivores and than could be expected from mouth gape data (Wysujack and Mehner 2005).

Table 1 List in alphabetical order of fish species (order, family, scientific and common names) encountered in the natural diet of *Silurus glanis*.

Order	Family	Scientific name	Common name	References ¹		
Acipenseriformes	Acipenseridae	<i>Acipenser gueldenstaedtii</i>	Russian sturgeon	(11)		
		<i>Acipenser stellatus</i>	Starry sturgeon	(11)		
		<i>Huso huso</i>	Beluga	(11)		
Anguilliformes	Anguillidae	<i>Anguilla anguilla</i>	European eel	(12)		
Atheriniformes	Atherinidae	<i>Atherina boyeri</i>	Big-scale sand smelt	(5, 11)		
Clupeiformes	Clupeidae	<i>Alosa</i> sp.	Shads	(5, 7, 8)		
		<i>Alosa pontica</i>	Danube shad	(14)		
		<i>Clupeonella delicatula</i>	Black Sea sprat	(11)		
Cypriniformes	Cobitidae	<i>Cobitis</i> spp.	Loaches	(1, 5, 8, 11)		
		<i>Misgurnus fossilis</i>	Weather loach	(14)		
		<i>Cobitis taenia</i>	Spined loach	(14)		
	Cyprinidae	<i>Abramis brama</i>	Common bream	(5–7, 9, 11, 12, 14)		
		<i>Alburnus alburnus</i>	Bleak	(1, 3, 5–9, 13, 14)		
		<i>Alburnoides bipunctatus</i>	Riffle minnow	(14)		
		<i>Aspius aspius</i>	asp	(5, 7, 14)		
		<i>Barbus brachycephalus</i>	Aral barbel	(2, 5)		
		<i>Barbus capito</i>	Bulatmai barbel	(1)		
		<i>Barbus lacerta</i>	Kura barbel	(1)		
		<i>Barbus borysthenicus</i>	Danube barbell	(14)		
		<i>Blicca bjoerkna</i>	Silver bream	(1, 5, 7–9, 12, 14)		
		<i>Capoeta capoeta</i>	Transcaucasian barb	(1)		
		<i>Capoetobrama kuschkewitschi</i>	Sharpray	(2)		
		<i>Carassius carassius</i>	Crucian carp	(6, 10, 13, 14)		
		<i>Chalcalburnus chalcoides</i>	Danube bleak	(1, 5)		
		<i>Chondrostoma oxyrhynchum</i>	Terek nase	(1)		
		<i>Chondrostoma soetta</i>	Apennian nase	(13)		
		<i>Cyprinus carpio</i>	Common carp	(5–8, 10, 11)		
		<i>Gogio gobio</i>	Gudgeon	(1, 9)		
		<i>Hemiculter</i> sp.	Sharpbelly	(10)		
		<i>Leuciscus cephalus</i>	Chub	(13)		
		<i>Pelecus cultratus</i>	Rasorfish	(7)		
		<i>Rhodeus amarus</i>	Bitterling	(5, 9)		
		<i>Rutilus aula</i>	Apennian roach	(13)		
		<i>Rutilus frisii kutum</i>	Caspian roach	(6)		
		<i>Rutilus rutilus</i>	Roach	(2, 3, 5–11, 14)		
		<i>Scardinius erythrophthalmus</i>	Rudd	(5–9, 11, 12, 14)		
		<i>Tinca tinca</i>	Tench	(4–8)		
		<i>Vimba vimba</i>	Vimba	(14)		
		<i>Vimba vimba persa</i>	Vimba sub-species	(6)		
		Esociformes	Esocidae	<i>Esox lucius</i>	Northern pike	(6–8, 14)
		Gasterosteiformes	Gasterosteidae	<i>Pungitius platygaster</i>	Southern stickleback	(5, 6, 8)
<i>Gasterosteus aculeatus</i>	Threespine stickleback			(14)		
Mugiliformes	Mugilidae	unidentified	Mulletts	(5)		
Perciformes	Centrarchidae	<i>Lepomis gibbosus</i>	Pumpkinseed	(9, 14)		
	Gobiidae	<i>Neogobius</i> sp.	Goby species	(5–8, 11, 14)		
	Percidae	<i>Gymnocephalus cernuus</i>	Ruffe	(3, 12, 14)		
		<i>Perca fluviatilis</i>	Eurasian Perch	(3, 6–9, 11–12, 14)		
		<i>Sander lucioperca</i>	Pikeperch	(4–5, 7–8, 11–12, 14)		
Petromyzontiformes	Petromyzontidae	<i>Caspiomyzon wagneri</i>	Caspian lamprey	(1, 5)		
Pleuronectiformes	Pleuronectidae	<i>Platichthys flesus</i>	Flounder	(13)		
Salmoniformes	Salmonidae	<i>Oncorhynchus mykiss</i>	Rainbow trout	(9)		
Siluriformes	Ictaluridae	<i>Ameiurus melas</i>	Black bullhead	(9)		
	Siluridae	<i>S. glanis</i>	European catfish	(4, 5, 7, 14)		

Table 1 Continued.

Order	Family	Scientific name	Common name	References ¹
Syngnathiformes	Syngnathidae	<i>Syngnathus nigrolineatus</i>	Black-striped pipefish	(11)
		<i>Nerophis ophidion</i>	Staight nosed pipefish	(14)

¹(1) Abdurakhmanov (1962); (2) Bekbergenov and Sagitov (1984); (3) Czarnecki *et al.* (2003); (4) Doğan Bora and Gül (2004); (5) Mamedov and Abbasov (1990); (6) Omarov and Popova (1985); (7) Orlova and Popova (1976); (8) Orlova and Popova (1987); (9) Pouyet (1987); (10) Mukhamediyeva and Sal'nikov (1980); (11) Stolyarov (1985); (12) Wysujack and Mehner (2005); (13) Rossi *et al.* (1991) and (14) Bruyenko (1971).

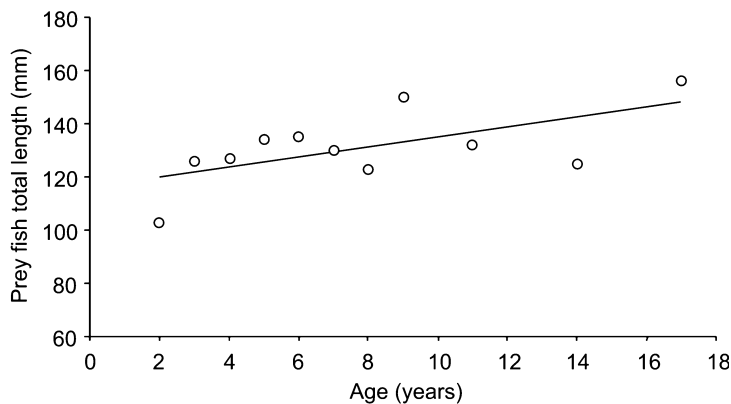


Figure 2 Prey fish (*R. rutilus*) total length (mm) and *S. glanis* age (years), $y = 1.86x - 116.49$, $F = 5.68$, $r^2 = 0.39$, $P = 0.04$. Calculated from Orlova and Popova (1987).

Ontogenetic changes in diet

The onset of exogenous feeding in *S. glanis* begins just before depletion of the yolk sac, on about the fifth day after hatching (Bruyenko 1971). After depletion of the yolk sac, *S. glanis* larvae and juveniles are very lively and voracious looking for food both on the bottom and in open water (Mihálik 1995). The diet of juveniles (4–7 cm TL) is varied, but sometimes is composed exclusively of invertebrates (Orlova and Popova 1987). However, the diet can also be composed of benthic or mid-water column organisms, e.g. Chironomidae, Hemiptera, Diptera, Coleptera, Mysidacea, Daphnidae (Bekbergenov and Sagitov 1984), as well as young-of-the-year (YoY) fishes (Table 2). The rapidly growing YoY *S. glanis* soon begin to look for larger items living on the bottom and in the littoral zone (Mihálik 1995). In *S. glanis* larvae of 11–20 mm TL, diet consists of Copepoda, Cladocera, Oligocheta and Tendipedidae, with Copepoda being most frequent food. Copepoda disappears from diet of *S. glanis* larvae of 21–34 mm TL. For *S. glanis* larvae, Oligocheta and Amphipoda are the most frequent food item (Bruyenko 1971). However, during their first year (5–12 cm TL), *S. glanis* take an increasing proportion of YoY fishes as prey

(Stolyarov 1985; Orlova and Popova 1987), with prey sizes ranging from 3.0–3.3 cm TL (Bruyenko 1971). Vegetal detritus can constitute up to 17.8% of juvenile diet (Theouov and Gousseva 1977). If food availability is low, then cannibalism can occur, with larger individuals taking smaller, less-developed specimens (Mihálik 1995). At age 2 years, *S. glanis* juveniles feed mainly on cyprinid fishes, although gammarid amphipods may represent about 10% of the diet (Orlova and Popova 1987; Tables 1 and 2), and in the Danube delta (Ukraine, Moldova), crayfish represent up to 67.3% of diet (Bruyenko 1971). Beginning at age 3 years (up to 30 cm TL), dietary breadth increases considerably, with the proportion of non-fish prey being elevated during ages 2+ to 4+ (i.e. 25–30%), but decreasing to 7–15% thereafter (Orlova and Popova 1987).

The predatory behaviour of adult *S. glanis* is apparent in the diversity of their diet, which is composed mainly of fish items (Tables 1 and 2) although this is highly dependant of the number of *S. glanis* specimens examined (Fig. 3). In some Spanish populations, the diet is based on red swamp crayfish (*Procambarus clarkii*, Astacidae) rather than fish (Carol 2007). The maximal fish prey diversity reported in a single study was 15 species (Orlova and Popova 1976), based on the examination of

Table 2 Review of *Silurus glanis* diet studies, with the number of specimens examined (n), the reported size and age ranges, and the number food items (fish, non-fish) listed in alphabetical order (Juv = juvenile, A = adult) and their proportions (%).

Source ¹	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)
<i>S. glanis</i> (n)	n/a	50	23	162	n/a	1850	10413	955	37	26	400	155	97	>2000
Size range (cm)	n/a	n/a	n/a	22–52	n/a	31–100	40–160	n/a	20–180	n/a	5–100	54–96	5–116	n/a
Age range (years)	n/a	Juv	>3+	0–5	n/a	n/a	n/a	2–12	n/a	n/a	Juv&A	n/a		0–26 %
Number of items														
Fish items (Family)														
Acipenseridae											3			7
Anguillidae												1		7
Atherinidae					1						1			14
Clupeidae					1		1	1			1		1	36
Cobitidae	2				1			1			1		2	36
Cyprinidae	8	3	2	1	11	9	9	6	7	4	4	4	5	100
Esocidae						1	1	1						29
Gasterosteidae					1	1		1						29
Mugilidae					1									7
Centrarchidae									1					14
Gobiidae					1	1	1	1			1			43
Percidae			2	1	1	1	2	2	1		2	3		71
Petromyzontidae	1				1									14
Salmonidae									1					7
Pleuronectidae													1	7
Ictaluridae									1					7
Siluridae				1	1		1							29
Syngnathidae											1			14
Totals	11	3	4	3	20	13	15	13	11	4	14	8	6	22
Non-fish items														
Invertebrates														
Nematoda – Cestoda				1									1	14
Scyphozoa														7
Crustaceans			1	1	1	2	1	2	1		1	1	1	79
Annelida														7
Insects		9		3						2	1		1	43
Molluscs				1								1	1	21
Plants										1				7
Vertebrates														
Birds			1			1	1					1		29
Frogs						1	1	1	1		1			36
Totals	0	9	2	6	1	4	3	3	2	2	3	3	4	10

¹(1) Abdurakhmanov (1962); (2) Bekbergenov and Sagitov (1984); (3) Czarnecki *et al.* (2003); (4) Doğan Bora and Gül (2004); (5) Mamedov and Abbasov (1990); (6) Omarov and Popova (1985); (7) Orlova and Popova (1976); (8) Orlova and Popova (1987); (9) Pouyet (1987); (10) Mukhamediyeva and Sal'nikov (1980); (11) Stolyarov (1985); (12) Wysujack and Mehner (2005), (13) Rossi *et al.* (1991), and (14) Bruyenko (1971).

10 413 specimens, with 20 species observed in >2000 examined *S. glanis* (Bruyenko 1971; Mamedov and Abbasov 1990). However, across a range of dietary studies on *S. glanis*, at least 47 fish species have been reported (Table 1) including freshwater

or diadromous, e.g. European eel (*Anguilla anguilla*, Anguillidae), Russian sturgeon (*Acipenser gueldenstaedtii*, Acipenseridae) species, as well as native or non-native species, e.g. pumpkinseed (*Lepomis gibbosus*, Centrarchidae), black bullhead (*Ameiurus*

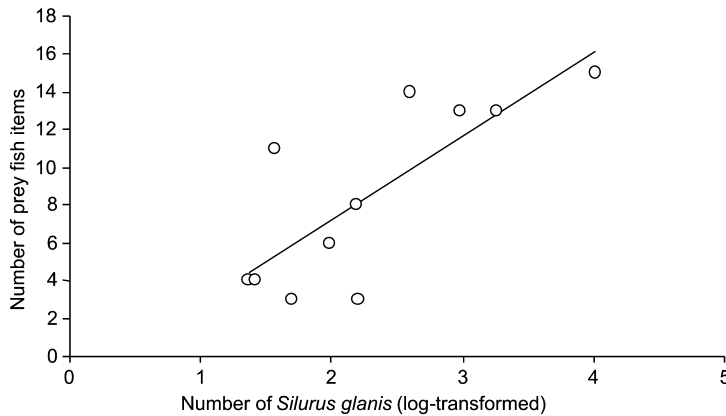


Figure 3 Number of prey fish items observed in the diet of *S. glanis* according to the number of individuals studied (data log-transformed, $y = 4.39x - 1.55$, $F = 13.80$, $r^2 = 0.61$, $P = 0.005$). See Table 2 for references of diet contents.

melas, Ictaluridae) (Abdurakhmanov and Kasymov 1962; Orlova and Popova 1976, 1987; Mukhammediyeva and Sal'nikov 1980; Bekbergenov and Sagitov 1984; Omarov and Popova 1985; Stolyarov 1985; Pouyet 1987; Mamedov and Abbasov 1990; Czarnecki *et al.* 2003; Doğan Bora and Gül 2004; Wysujack and Mehner 2005). Species of the family Cyprinidae were recorded as prey in all of the 14 studies of *S. glanis* diet subjected to review (Table 2) and represented half of the 54 reported prey species of *S. glanis*. Percidae (three species) occurred in 71% of the reviewed studies (Table 2), followed by Gobiidae (43%), Cobitidae and Clupeidae (both 36%), with cannibalism reported in 29% of the investigations. Non-fish prey items were reported in virtually all studies including vertebrates, invertebrates or plants (Table 2): crustaceans (79% of the studies; specifically crayfish = up to 57%), Amphibia (specifically frogs: 36%), insects (43%) and birds (29%, especially young waterfowl). Exceptional prey items include small mammals such as rodents (Wheeler 1969; Lever 1977; Greenhalgh 1999; Czarnecki *et al.* 2003).

Seasonal changes in diet

The intensity of food intake and the rate of metabolism are mainly dependant on water temperature. For this reason, food intake is most intensive during the spring and generally falls to a minimum in winter (Mihálik 1995). The proportion of empty stomachs decreases considerably with increasing water temperature (Wysujack and Mehner 2005), emphasizing the link between thermal conditions and prey abundance, which can vary between regions (Omarov and Popova 1985). In the Volga delta and the Arakum Reservoir within the River Terek delta, feeding season generally lasts about 8 months (Fig. 4), starting in spring with the most intensive feeding taking place in April to May and also in August (Orlova and Popova 1976; Omarov and Popova 1985). But, there have been reports (reviewed in Omarov and Popova 1985) of feeding seasons lasting all year in the Kura River and also of winter as the main feeding period, for example in the Tsimlyansk Reservoir on the River Amur-Dar'ya.

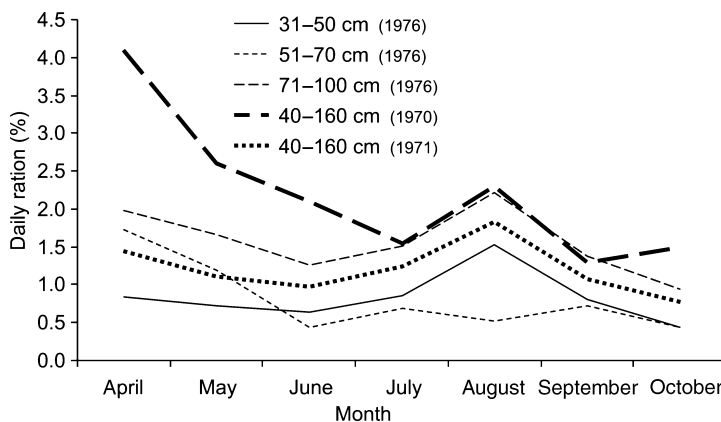


Figure 4 Monthly evolution from April to October of the mean daily ration, expressed as a percentage of body weight (%) of *S. glanis* of variable size ranges. Fish were sampled in 1970 and 1971 in the Volga Delta (from Orlova and Popova 1976) and in 1976 in the Arakum reservoirs (from Omarov and Popova 1985).

Nonetheless, in native populations, the seasonal increase in feeding usually begins when waters start to warm in spring, when prey species start to become abundant, such as with the spawning of migratory species (Bruyenko 1971; Omarov and Popova 1985; Orlova and Popova 1987). At this time, only about 43–52% of *S. glanis* stomachs are empty (Omarov and Popova 1985). Food availability drops during June–July (Fig. 4), as semi-migratory fish move to deeper waters and feeding intensity of *S. glanis* incidentally declines, with about 70–78% of *S. glanis* having empty stomachs (Orlova and Popova 1976; Omarov and Popova 1985). With the continued rise in water temperatures during August, the availability of the riverine fishes is the highest and feeding intensity rises to the point where only 20–25% of *S. glanis* were found to have empty stomachs (Omarov and Popova 1985). Feeding intensity usually drops significantly from September as temperatures decrease and ceases completely when temperatures are below 7–12 °C (Abdullayev *et al.* 1978; Omarov and Popova 1985). In fact, the species practically does not feed from November to March (Bruyenko 1971; Omarov and Popova 1985), when it hibernates in deep holes among tree roots (Greenhalgh 1999).

Comparable seasonal variations in feeding habits seem to be observed outside of its native range, although dietary data on introduced populations is very limited (Pouyet 1987; Rossi *et al.* 1991; Carol 2007). Of particular interest in recent studies made between March 2003 and June 2006 of *S. glanis* diet in reservoirs and canals of northeast Spain (Catalan region) was the predominance in terms of percentage biomass of non-native crayfish and fish species in the diet (Carol 2007). Iberian endemic fishes are not adapted to the conditions in the man-made reservoirs, where non-native species normally dominate the fish assemblages (Godinho *et al.* 1998; Carol *et al.* 2007a). Introduced *P. clarkii* was present in *S. glanis* diet from all Catalan study sites, which included man-made canals of the Ebro delta and river reservoirs, exceeding 80% (in biomass) of the diet in one reservoir (Carol 2007). Of the non-native fishes, *C. carpio*, *R. rutilus* and bleak (*Alburnus alburnus*, Cyprinidae) made up the greatest percentage of the biomass, with other non-native species, i.e. *S. lucioperca*, *L. gibbosus*, largemouth bass (*Micropterus salmoides*, Centrarchidae), representing up to 15% of the biomass in one reservoir. The only endemic species forming a high proportion of the

biomass was the Iberian barbel (*Barbus graellsii*, Cyprinidae) and this was in the artificial canals of the Ebro delta only (Carol 2007).

Age and growth

Age and ageing

The age of *S. glanis* is usually estimated by the analysis of sections of the pectoral bony fin ray (Harka 1984; Harka and Bíró 1990; Horoszewicz and Backiel 2003) or less frequently using vertebrae and otoliths (Planche 1987a, b; Rossi *et al.* 1991; Fig. 5). Horoszewicz and Backiel (2003) found, with reared fish of known age, that some fish may display juvenile rings that are not true annuli. They also suggested that the growth of the haemal tube of the ray may damage the first annuli. For purposes of growth back-calculation, Harka and Bíró (1990) recommend the measurement of 'oral radii' instead of the larger caudal stems, because of allometric growth and hence possible biases.

Ontogeny and growth

S. glanis is a species characterized by a high growth rate (Orlova 1989), with the greatest production and consumption in juveniles (Raat 1990). Growth is most intensive in the first year of life and yearlings can reach 38–48 cm TL (Orlova 1989). Intensive growth will carry on until about the age 6 or 7 after which the rate gradually decreases. Mean TL ranges 20–30 cm after 1 year (Wheeler 1969; Maitland and Campbell 1992), then about 40 cm TL at age 2, reaching 100 cm TL by 6–7 year (Wheeler 1969). With the onset of sexual maturation in age 3–4 year old fish, the annual increase in body length decreases down to 5–7 cm by age 14 (Orlova 1989). Growth in weight is quite slow in the first few years and then increases with age staying relatively high until the age of 20–30 years (Hochman 1966). The relative increase of weight is very high in maturing fish averaging 30% as compared to 6–10% of TL (Orlova 1989).

S. glanis growth takes place in annual spurts, usually during the warmer months of the spring and summer (Maitland and Campbell 1992), and as such is food and water temperature dependent (Lelek 1987; Greenhalgh 1999). Temperature actually regulates all metabolic processes from digestion, assimilation and egestion of food and *S. glanis* cannot digest food below 10 °C. The optimum

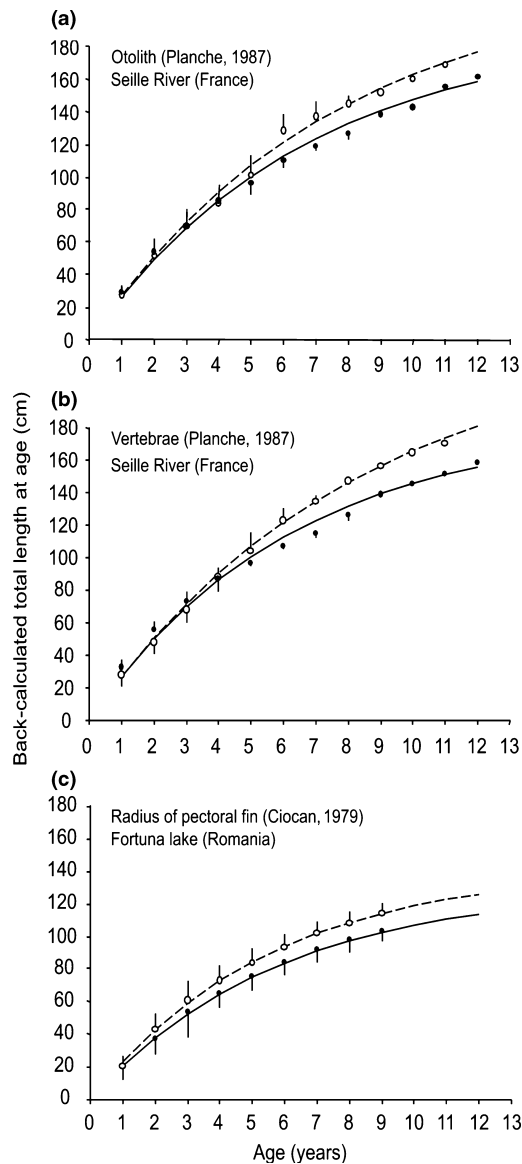


Figure 5 Back-calculated total length (cm) at age (year) of *S. glanis* for males (○) and females (●). Fish were aged using three different tissues: (a) otolith ($n = 25$), (b) vertebrae ($n = 19$) and (c) radius of the pectoral fin ($n = 1165$). The von Bertalanffy growth curves are presented for males (dotted line) and females (full line). The errors-bars represent the standard deviations. Adapted from Planche (1987a, b) and Ciocan (1979).

temperature for growth and food conversion is in the range of 25–28 °C and food assimilation is reduced by half when water temperatures fall from 23–15 °C (Hilge 1985). Apart from natural influences, man-made factors such as fishing or water

pollution can also affect the growth of *S. glanis* (Mihálik 1995).

Inter-annual growth is highly irregular, both within and between cohorts, and these year-to-year variations are most likely related to fluctuations in favourable abiotic factors, such as temperature, food abundance or hydrological regime (Harka 1984). Variations in growth may even be because of the condition of the individual or migration into a microhabitat with more or less favourable feeding conditions (Hochman 1967) and cannibalism has been associated with higher growth rates in some cases.

Sexual growth dimorphism

Contrary to relative growth, most studies of *S. glanis* longitudinal growth show that males have a higher growth rate than females (Fig. 5) and reach sexual maturity earlier. There is also a difference in mass growth rate between the sexes for the same length: males always have greater mass than females of the same age (Ciocan 1979). Overall, *S. glanis* growth rates are relatively similar for both sexes until the age of 4 or 5 years after which male growth increases considerably (Mohr 1957; Planche 1987a, b). However, some studies have reported differences at age 2 years (Ciocan 1979) and even by the end of the first year (Hochman 1967); differences between males and females were of about 5.5 cm TL at the end of the juvenile period, but this gap closes as males achieve maturity at about age 4, whereas female growth rates of the same age remain constant until maturity is reached, when growth also reduces (Hochman 1967). At age 10 years, differences between sexes are about 10 cm in Danish waters (Hochman 1967), with a length difference of 15 cm found in specimens of age 16+ (Mihálik 1995); at age 18+, the difference is about 20 cm (Bizjaev 1952). Therefore, the variations in body length and growth are wide and become greater with age (Harka 1984). Life span is 22 years for males and 16 years for females in the Volga Delta (Orlova 1989), with specimens of 26 years old having been observed in the Danube delta (Bruyenko 1971).

Geographical variation in growth rates

Growth in *S. glanis* is highly variable (Harka 1984), depending upon habitat. In cool conditions, a 10-year-old *S. glanis* may only weigh 2 kg

(Greenhalgh 1999). Similarly, a specimen of 890 mm TL might be fast growing and aged 5 or slow growing and aged 9. As with length, there is much variation in the weight of individuals of the same age and same length (Hochman 1966; Ciocan 1979). Relatively rapid growth reported for *S. glanis* in Hungarian waters (Antos 1970; Antal-Tölg 1971) contrasts with the considerably slower growth rates (Table 3) reported for waters of the former Czechoslovakia (Hrbáček *et al.* 1952; Balon 1966; Hochman 1966; Sedlár and Geczö 1973; Tandon and Oliva 1977; Rossi *et al.* 1991). According to Harka (1984), *S. glanis* is the largest fish species inhabiting Hungarian waters, with early literature stating weights of 200–250 kg and lengths up to 3 m TL. The upper limit is 3.5 m TL in the River Tisza, but currently, *S. glanis* of ≥ 2 m TL are scarce. This has been attributed to various factors, for instance, reduced food supply and increased fishing intensity, but not to the genetic make-up of the species.

The largest and heaviest *S. glanis* reported in the literature were caught in the River Dnepr, where a maximum record of 5 m TL and 306 kg has been recorded near Kremenchuk (Berg 1949). *S. glanis* weighing ≈ 300 kg are no rarity in the River Volga and the Caspian Sea (Mihálik 1995), with specimens of ≈ 200 kg also being not so rare in the rivers Tcho and Syr-Darya, and *S. glanis* can exceed 2 m TL and 130 kg body weight in the Aral Sea basin (Zholdasova and Guseva 1987). In the rivers Nitra, Váh, Danube and Theiss, *S. glanis* growth was reported to be practically the same (Sedlár 1987), although growth in the River Theiss was a little faster than in the rivers Danube and Váh. Hochman (1966) estimated that if all optimal conditions were met, then *S. glanis* could reach a size of 1.2–2.5 kg after 3 years in a natural environment. To compare the growth performance of native and introduced populations of *S. glanis* (Table 3), the von Bertalanffy model (Ricker 1975) was applied to these data following Copp *et al.* (2004) in which the index of growth (in length) performance ϕ' (Munro and Pauly 1983) was derived using von Bertalanffy parameters. $\phi' = \log_{10}[k] + 2 \log_{10}[L_{\infty}]$, where k is the rate at which asymptotic length, L_{∞} , is approached. No clear relationship with latitude was observed, but the growth trajectory of introduced populations, with a caveat for small sample size ($n = 3$, France, Italy, UK), appears to be higher in France and Italy than in the native range (Fig. 6), but in the UK, growth appears to be slower (Britton

et al. 2007). There does appear to be some effect of latitude in the three introduced populations, with TL at age being greater at lower latitudes in all ages except 1+ and 2+ (Table 3). Of these, note that the River Seille (France) population is included amongst the non-native populations because it is known to have been introduced into the Rhône catchment in 1857 after being absent since the Miocene or up to 2 million years ago. Condition factors are not often reported, but in the Khauzkhan Reservoir (Mukhamdiyeva and Sal'nikov 1980), *S. glanis* were reported to have Fulton's condition values of 0.48–1.11 (mean = 0.77), with Clark's condition values of 0.46–0.96 (mean = 0.68).

Reproduction

A cyclic process controlled by hormones, reproduction in *S. glanis* is influenced by environmental factors such as temperature and day length (Maitland and Campbell 1992). Having over-wintered in deep, slow-moving areas of the main channel, *S. glanis* move at the end of March–April, when temperatures are 8–10 °C (Berg 1949; Shikhshabekov 1978) undertaking short-distance migrations upstream to spawning grounds (Lelek 1987). In the lower River Danube, this migration is reported to take place in February and March at water temperatures of 4–6 °C (Ciocac 2004). In Central Europe, this migration generally takes place from the end of March to the beginning of April and in Eastern Europe, from the end of May until June. Pairing up of males and females takes place during the migration, so *S. glanis* arrives at the spawning site already in pairs (Mihálik 1995). Spawning begins when water temperatures reach a minimum temperature of 18–22 °C (Mohr 1957; Lever 1977; Shikhshabekov 1978) and occurs in the vegetated, marshy zones of lakes and flood plains (Wheeler 1969), such as in the deltas of wide rivers (Berg 1949). Preferred spawning substrata for *S. glanis* are riparian tree roots at moderate depths, which serve to provide shelter for the eggs (Lelek 1987). The spawning season lasts from mid-May to mid-June in the south of its range and from July to August in the north (Greenhalgh 1999). In reservoirs of the Dagestan region, the spawning of *S. glanis* extends over 2 months with no mass spawning (Shikhshabekov 1978) because the brood stock migrate into the spawning areas at different times. Similarly, the spawning period in the Manzelet Reservoir (Turkey) is even longer, extending from early June to August

Table 3 Back-calculated total length (TL) at age of *Silurus glanis* populations from various sources in its native (upper part) and introduced (lower part) ranges.

Site	TL at age																									Ref. ²
	C	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	25				
L. Dengizkul'	UZ	18	35	60																				(1)		
L. Zeykul'	UZ	22	36	47																				(1)		
L. Korpkul'	UZ	23	35	43																				(1)		
Faikhad Res.	n/a	30	36	41	57																			(2)		
L. Shorkul'	UZ	19	38	55	63	75																		(1)		
R. Vah	CZ	19	33	54	73	83																		(3)		
R. Nitra	SK	13	30	55	78	95	110																	(3)		
R. Vah	CZ	16	25	39	50	60	66																	(4)		
R. Nitra	SK	16	29	40	51	58	60																	(3)		
L. UlilShorkul'	UZ	22	39	54	63	69	78																	(1)		
L. Karakyr	UZ	28	43	58	63	72	76																	(1)		
R. Dyje	CZ	14	33	50	65	75	88	96																(4)		
L. Matita	RO	17	30	41	52	61	69	76																(4)		
L. Gorgova	RO	19	36	51	62	71	77	81																(4)		
Aral Sea	n/a	19	30	41	51	61	71	78																(5)		
L. PuiuPuiulet	RO	20	38	53	68	80	89	90																(4)		
L. Yaskha	TM	23	37	49	60	69	77	89																(6)		
Volga Delta	RU	-	51	59	65	71	76	81	87															(7)		
L. Tuzgan	UZ	28	45	59	66	78	87	94	100															(1)		
Volga Delta	RU	35	58	66	76	84	92	100	106															(8)		
R. Vah	CZ	11	24	36	47	55	63	70	76	81														(4)		
L. Fortuna	RO	20	40	57	69	80	89	97	103	108														(4)		
Aral Sea	n/a	-	30	41	52	62	72	86	91	99	107													(9)		
Kakhovka Res.	UA	-	42	71	86	91	95	97	107	110	130													(10)		
R. Ural	RU	-	58	66	72	82	96	102	108	117	136													(11)		
R. Danube	CZ	14	27	43	60	69	76	75	76	78	80													(3)		
R. Tisza	HU	14	25	37	47	59	70	82	88	92	96													(12)		
L. Lion	CZ	17	37	52	66	74	82	88	94	101	102													(12)		
Kuybyshev Res.	RU	17	29	48	59	75	86	95	103	111	117													(13)		
L. Amudar'ya	n/a	19	27	34	44	54	64	76	90	101	115													(14)		
L. Balkhash	KZ	24	43	57	68	79	91	97	103	109	115													(15)		
Tsimlyansk Res.	RU	29	45	58	70	81	91	100	108	117	124													(16)		

Table 3 Continued.

Site	TL at age																									Ref. ²
	C	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	25				
R. Danube	n/a	32	56	74	85	96	102	111	118	131	138													(17)		
Asod canal	SK	12	24	33	43	53	63	72	72	78	88	92												(3)		
R. Danube	CS	28	38	47	58	76	88	102	119	129	140	160												(18)		
R. Berounka	CZ	-	-	90	96	100	105	112	118	139	139	145	159											(5)		
R. Ural	RU	41	57	74	92	97	113	-	-	153	-	-	175											(19)		
R. Nitra	SK	13	25	39	51	59	69	77	83	95	112	120	124	130	133									(20)		
Zegrzynski Res.	PL	19	33	47	62	76	83	85	95	97	107	109	116	122	122									(21)		
R. Vistula	PL	21	39	58	70	82	92	101	109	115	122	127	131	132	146									(21)		
R. Aral Sea	n/a	-	-	61	65	72	79	86	92	104	111	112	127	130	136	148								(5)		
Vranov Res.	CZ	11	24	37	49	60	71	84	99	108	118	128	147	153	158	166								(4)		
R. Aral Sea	n/a	18	29	40	50	61	71	78	87	92	99	97	102	117	117	125								(22)		
L. Aral (Muinak)	KZ	-	61	65	72	79	86	92	104	111	112	127	130	136	148	140	175	195	-	-	-	220		(23)		
Orlik Res.	CZ	13	25	39	53	64	75	85	93	101	109	115	122	127	133	139	144	150	155	160	165			(24)		
Undefined waters	RO	17	28	39	49	60	71	84	93	101	110	-	119	-	-	150	-	164	-	-	186			(25)		
R. Tisza	HU	18	32	46	59	71	84	95	107	117	128	138	147	156	165	174	182	190	197	204	211			(26)		
R. Don	RU	23	55	76	91	106	118	129	138	148	155	165	172	180	190	194	197	208	212	216	227			(27)		
R. Vah	CZ	11	24	36	47	55	63	70	76	81	87	95	99	106	111	121	-	-	-	-	-	207		(28)		
Various waterways	RU	12	22	36	48	60	71	80	88	96	103	-	-	-	136	-	-	-	-	-	171	199		(29)		
Centhus dead arm	SK	15	29	39	43	52	61	72	84	93	99	106	113	122	132	138	-	-	-	-	167	180		(30)		
Mean native range:		20	36	51	62	72	81	88	97	106	113	120	130	130	138	147	166	177	190	193	192	198				
River P6	IT	19	44	78	-	110	127	-	-	-	215													(31)		
River Seille ¹	FR	28	53	70	85	99	119	128	136	145	151	162	161											(32)		
an English Lake	UK	-	-	-	64	78	86	93	98	102	106	110	113	116	119	121								(33)		
Mean introduced range:		24	49	74	75	96	111	111	117	124	157	136	137	116	119	121										

L, Lake; Res, Reservoir; R, River.

¹Population re-introduced in 1857 after a long geological absence.²References: (1) Abdullayev et al. (1978); (2) Maksunov (1961) in Abdullayev et al. (1978); (3) Hochman (1967) in Sedlář and Gečzö (1973); (4) Ciocan (1979); (5) Berg (1949); (6) Aliyev (1953) in Abdullayev et al. (1978); (7) Orlova (1989); (8) Fortunatov and Popova (1973) in Orlova (1989); (9) Mikhin (1931) in Lysenko (1978); (10) Probatova (1967) in Lysenko (1978); (11) Voynova (1973) in Lysenko (1978); (12) Sedlář (1987); (13) Vasyanin (1972) in Lysenko (1978); (14) Serov (1948) in Lysenko (1978); (15) Lysenko (1978); (16) Dronov (1974) in Lysenko (1978); (17) Bruyenko (1967) in Lysenko (1978); (18) Ristic (1977) in Harka (1984); (19) Probatov (1929) in Berg (1949); (20) Sedlář and Gečzö (1973); (21) Horoszewicz and Backiel (2003); (22) Oliva et al. (1951) in Mihalák (1995); (23) Berg (1933); (24) Hochman (1965) in Harka (1984); (25) Gyurkó (1972) in Harka (1984); (26) Harka (1984); (27) Bizjaev (1952) in Harka (1984); (28) Sedlář (1987); (29) Tandon and Oliva (1977); (30) Balon (1966), a dead arm of the River Danube; (31) Rossi et al. (1991); (32) Planche (1987a, b); (33) Britton et al. (2007).

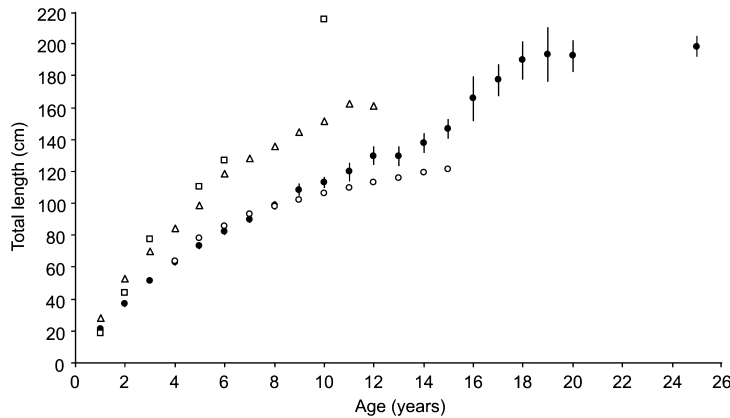


Figure 6 Mean back calculated total length (cm) at age (years) of *S. glanis* in the native range (●) and the introduced range, which includes France (△, from Planche 1987b), Italy (□, from Rossi *et al.* 1991) and the United Kingdom (○, from Britton *et al.* 2007). The error bars are standard errors. See Table 3 for details.

(Alp *et al.* 2004). After the spawning period is over, *S. glanis* moves back down the river to recover from spawning and then enters deeper waters (Lelek 1987). Although *S. glanis* shows a very limited home range and migrations are not usually extensive, migrations to find a spawning partner may be more extensive in water courses with recent introductions and/or where *S. glanis* densities are low.

Sexual maturation and gonad development cycle

Age at maturity in *S. glanis* is generally reported as being 3–4 years old, with mean length at maturity ranging from 39 to 71 cm TL (Probatov 1929; Hochman 1967; Zharov 1969; Abdullayev *et al.* 1978; Shikhshabekov 1978; Mukhamediyeva and Sal'nikov 1980; Orlova 1989), although *S. glanis* in the Volga Delta have been reported to begin maturing at age 2 (mean TL = 50.7 cm, mean weight = 1.22 kg), with practically all fish mature at age 6, with mass maturation occurring in ages 3–4, corresponding to 57–66 cm TL and 1.3–2.3 kg weight (Orlova 1989). Males mature earlier than the females, at a minimum size of 78.8 cm TL and at age 3, whereas females mature at a minimum size of 87.1 cm TL and at age 4 in the Menzelet Reservoir in the East Mediterranean region of Turkey (Alp *et al.* 2004). In an adult *S. glanis* weighing 6–10 kg, the gonad represents only 9–15% of the total body weight, which is a relatively small proportion (Mihálik 1982).

Testicles are composed of a pair of glands situated in the dorsal part of the main cavity. The two glands look like flattened ribbons (Planche 1987b). When sexually immature, the glands are pale pink and in mature individuals they have a whitish colour (Shikhshabekov 1978). Testicular

mass relative to body mass is very low in this species (Hochman 1967; Shikhshabekov 1978). Male *S. glanis* may have running milt 30–40 days prior to spawning and they are reported to produce sperm for a relatively long period (Hochman 1967; Shikhshabekov 1978), with a gradual, extended duration of spermatozoa discharge being a peculiarity of male *S. glanis*, which are never completely spent (Shikhshabekov 1978).

Ovaries are linked together in the caudal part of the body and occupy only the posterior region of the main cavity. In female juveniles, the ovaries are more or less cylindrical and flatten slightly dorso-ventrally with age. When sexual maturity is reached, the ovaries extend into the proximal direction of the abdominal cavity. In comparison with other fish species, the ovaries are relatively small in size (Hochman 1967). In the Menzelet Reservoir (eastern Turkey), each gram of *S. glanis* ova consisted of 195 eggs prior to the spawning season (Alp *et al.* 2004). The eggs are large, pale yellow, 1.0–3.6 mm in diameter (Shikhshabekov 1978; Alp *et al.* 2004) ranging 0.7–2.5 mm in the Khauzkhan Reservoir, Turkmenistan (Mukhamediyeva and Sal'nikov 1980) and covered in a viscous, adhesive jelly-like membrane (Lukšienė and Svedäng 1997) including a muco-follicle epithelium that enables attachment of the eggs to the substrate. Eggs may also be placed in clusters and protected by the male (Riehl and Patzner 1998). Egg size varies monthly and correlates negatively with the number of eggs in the ovary (Alp *et al.* 2004). Indeed, the size of the eggs is dependent on the state of gonad development and on the size, age and condition of the fish (Hochman 1970). For example, in the Vranov Dam Reservoir, the largest eggs, which means the lowest number of eggs·g⁻¹ gonad, were

detected in the fastest growing and developing fishes (Hochman 1967).

Reproductive behaviour

Spawning usually occurs at night, when the water temperature has reached a maximum of 22–23 °C (Mihálik 1995). The best conditions for spawning are reported to be on warm sultry evenings characterized by a sudden drop in barometric pressure (Hochman 1970; Lever 1977), often just before a thunderstorm (Mihálik 1995). Leading up to this, competition for spawning areas increases with males developing aggressive behaviour and some individuals may become injured as a result (Planche 1987a). In 40–60 cm of water, the male excavates a nest (Mihálik 1982), which may be a scraped-out shallow hollow in weedy gravel or sand (Maitland and Campbell 1992), amongst fine roots of plants that hang freely in the water (Mihálik 1982) or simply a depression in a weed bed created by the male pressing on the plants (Shikhshabekov 1978).

Spawning is accompanied by a nuptial display (Planche 1987a). Males pursue females just under the water surface, and spawning will occur the same evening or the next day. The male nudges the female in the anal region, swims under her and may lift her so that her back is above water, the male wraps himself around the female for 10–12 s, the two then separate with the female sinking slowly to the bottom discharging 25 000–33 000 eggs kg⁻¹ of body weight in the nest (Lever 1977), with a range of values of approximately 11 600–26 400 eggs kg⁻¹ reported for *S. glanis* in the Khauz Khan Reservoir, Turkmenistan (Mukhamediyeva and Sal'nikov 1980). The male immediately follows to release milt to fertilize the eggs (Mihálik 1982). Spawning is repeated several times at certain

intervals and is accompanied by much noise and splashing. After 1.5–2.0 h, the spawning episode ceases (Mihálik 1995). Females differ in the type of spawning, with single batches reported for water bodies in the lower reaches of the River Terek (Shikhshabekov 1978) and in the outer delta of the Volga (Orlova 1989); multiple batches have been reported for the lower reaches of the Amudar'ya, where spawning did not occur every year (Zholdasova and Guseva 1987).

The male guards the eggs during the incubation period, even during the day, moving his tail fin every 3–5 min to ventilate the eggs and ensure an adequate oxygen supply until they hatch, which may be 2–10 days later depending on temperature (Maitland and Campbell 1992; Greenhalgh 1999). At 23–25 °C (water temperatures), the embryos hatch after 2.5–3.0 days (Mihálik 1995). *S. glanis* larvae are light sensitive and die in direct sunlight and also if water temperature falls below 13–14 °C (Mihálik 1982).

Absolute and relative fecundity

The absolute fecundity of female *S. glanis* ranges from 14 600 to 354 000 eggs (Shikhshabekov 1978; Mukhamediyeva and Sal'nikov 1980; Mihálik 1995). The considerable variability in *S. glanis* absolute fecundity is evident in the reports from its native range (Table 4). For example, in females of 105 cm TL, absolute fecundity ranges from 98 000 to 259 700 eggs depending on the geographic location (Hochman 1967). Indeed, values reported for female *S. glanis* in the lower reaches of the Zarafshan River in central Uzbekistan and Khorezm Province (North west Uzbekistan) were found to be low relative to those from the Kayrak-Kum Reservoir (Zharov 1969) and the lower reaches of the River

Table 4 Review of absolute fecundity estimates in female *Silurus glanis* within specified body total length (TL) and weight (kg) ranges (lower and upper values given).

Location	Number of eggs		Total length		Body weight		Source ¹
	lower	upper	lower	upper	lower	upper	
Dnieper Delta (former USSR)	136 000	467 000	97	134	6.7	18.0	(1)
Khauz Khan Reservoir (Turkmenistan)	96 250	353 910	100	125	8.3	13.4	(2)
Orlik Dam Reservoir (former Czechoslovakia)	7930	24 433	110	140	–	–	(3)
Orlik Dam Reservoir (former Czechoslovakia)	42 822	391 411	82	156	–	–	(3)

¹(1) Berg (1949); (2) Mukhamediyeva and Sal'nikov (1980); (3) Hochman (1967).

Volga (Suvorov 1948). The highest estimated absolute fertilities reported are 500 000–700 000 eggs noting that fecundity declines after a certain age (Hochman 1967). Fecundity estimates reported for *S. glanis* specimens of unspecified size include: >16 000 eggs in a small individual from the Vranov Reservoir, former Czechoslovakia (Hochman 1967), 9033 to 340 461 eggs per fish in the Menzelet Reservoir, eastern Turkey (Alp *et al.* 2004) and the rather low value of 8257 eggs in one spawning fish from Slapy Reservoir, former Czechoslovakia (Hochman 1967).

Relative fertility is equally variable and is influenced by food availability and water temperature (Hochman 1967) as well as on fish length and geographic origin. Estimates of relative fecundity range 7–42 eggs g⁻¹ weight (mean = 29 eggs g⁻¹) of fish (Shikhshabekov 1978). For example, in the Menzelet Reservoir (eastern Turkey), mean relatively fecundity was 8.4 ± 1.1 eggs g⁻¹ (Alp *et al.* 2004).

Parasites and pathogens

Viruses and bacteria

The majority of papers dealing with the viruses and bacteria of *S. glanis* are related to aquaculture or experimental conditions. It is reasonable to extrapolate challenge studies that have used natural routes of challenge (e.g. bath challenge) to assess the susceptibility of wild populations. However, disease is the outcome of the interaction of the pathogen, host and environment (Dohoo *et al.* 2003), which in aquaculture does not resemble the natural environment (e.g. differences in stocking density and water quality). Thus, information on diseases in farmed populations can only be extrapolated with caution to wild *S. glanis*. Mortality and morbidity in farmed fish is more likely to be observed and investigated than in the wild, where dead fish are quickly scavenged and only large-scale mortality or sharp declines in population levels are likely to attract attention. For example, a rapid decline in wild populations of *A. melas* in Italy has been attributed to a herpes virus infection, similar to channel catfish (*Ictalurus punctatus*, Ictaluridae) virus (Hedrick *et al.* 2003) to which *S. glanis* is resistant (Plumb and Hilge 1987).

The first report of an iridovirus (genus *Ranavirus*) causing mortality in *S. glanis* was from a farm in Germany where the virus caused 100% mortality in 11 day old YoY (Ahne *et al.* 1989). The virus was

named European sheatfish virus (ESV), and the susceptibility of *S. glanis* to ESV was established experimentally (Ahne *et al.* 1990). ESV is known to affect *S. glanis* only, though little work has been done to establish the susceptibility of other species and there are no recent reports of ESV causing problems in *S. glanis* hatcheries. ESV is closely related to other iridoviruses (e.g. frog virus 3; Ahne *et al.* 1998), and the spread of ESV is likely to follow the increased use of *S. glanis* in aquaculture and sport fishing.

Viral pathogens from the family of Rhabdoviridae, which includes viral haemorrhagic septicaemia and infectious haematopoietic necrosis, known to have strong impacts on salmonid fishes, have been linked to elevated mortality levels in young farmed *S. glanis* <8 weeks old at no less than six farms (Fijan *et al.* 1984; Békési *et al.* 1987). The virus has been identified as spring viraemia of carp (SVC), and therefore *S. glanis* is listed as a susceptible species (O.I.E. 2006). However, there are no recent reports of SVC in wild or farmed *S. glanis* populations. SVC is notifiable to the *Office International des Epizooties* (O. I. E.) and parts of Europe are free of the virus or have strict control programmes (e.g. UK). The movement of *S. glanis* may introduce SVC to new regions. SVC can cause high levels of mortality in immunologically naïve populations of *C. carpio*.

A number of bacterial species, which are ubiquitous in the aquatic environment, have been identified as causes of morbidity and mortality in farmed *S. glanis*. An example would be outbreaks in YoY *S. glanis* of *Flexibacter columnaris* (Farkas and Oláh 1980) and of *Vibrio* spp. in week old farmed fish (Farkas and Malik 1986). Other reports from aquaculture include systemic amoebiasis infections (Nash *et al.* 1988) with *Aeromonas* species (Farkas and Oláh 1982); flavobacterium species (Farkas 1985), a pasteurella-like bacterium (Farkas and Oláh 1984) and *Edwardsiella tarda* (Caruso *et al.* 2002). As all these bacterial species are widespread in aquatic environment, they will not be the cause of significant impact if transferred to the wild with movement of fish except perhaps under adverse (localized) environmental conditions.

Eukaryotic parasites

In contrast to viruses and bacteria, parasites of *S. glanis* have been examined in many countries as part of parasitological surveys of fish populations. At least 52 species of parasitic fauna have been identified in *S. glanis* (Table 5), though this is

Table 5 Eukaryotic parasites of *S. glanis* with host specificity, known geographical distribution and number of records for *S. glanis*.

Taxonomic groupings Parasite species	Family	Host specificity and known geographical distribution	Records for <i>S. glanis</i>
Microbial eukaryotes (former Protozoa)			
Apicomplexa			
<i>Eimeria siluri</i>	Eimeriidae	Rare specialist ¹ , Uzbekistan	1, 2
<i>Desseria turkestanica</i>	Haemogregarinidae	Rare specialist, Asia	2
Ciliophora			
<i>Trichodina acuta</i>	Trichodinidae	Generalist ² , widespread	2
<i>Trichodina nigra</i>	Trichodinidae	Generalist, widespread	2
<i>Trichodina siluri</i>	Trichodinidae	Specialist, Asia	2
<i>Trichodinella epizootica</i>	Trichodinidae	Generalist, widespread	2
Euglenozoa			
<i>Trypanoplasma ninaekohljakimovi</i>	Bodonidae	³	2
<i>Trypanosoma markewitschi</i>	Trypanosomatidae	Clariidae specialist, Asia	2
Microsporidia			
<i>Glugea tisae</i>	Glugeidae	Rare specialist, Eurasia	2, 3
Metazoa			
Acanthocephala			
<i>Acanthocephalus anguillae</i>	Echinorhynchidae	Generalist, Eurasia	4, 5
<i>Acanthocephalus lucii</i>	Echinorhynchidae	Generalist, Eurasia	5
<i>Acanthocephalus clavula</i>	Echinorhynchidae	Generalist, Eurasia	4
<i>Corynosoma caspicum</i>	Polymorphidae	Specialist, Asia	6
<i>Leptorhynchoides plagicephalus</i>	Rhadinorhynchidae	Acipenseridae specialist, Eurasia	4
<i>Pomphorhynchus laevis</i>	Pomphorhynchidae	Generalist, Eurasia	4, 5
Arthropoda			
<i>Argulus coregoni</i>	Argulidae	Generalist, Eurasia	5
<i>Argulus foliaceus</i>	Argulidae	Generalist, Eurasia	5
<i>Ergasilus sieboldi</i>	Ergasilidae	Generalist, widespread	5
<i>Lamproglana pulchella</i>	Lernaeidae	Generalist, Eurasia	7
<i>Pseudotracheilastes stellifer</i> ⁴	Lernaeopodidae	Specialist, Eurasia	5
Cnidaria			
<i>Myxobolus exiguus</i>	Myxobolidae	Generalist, widespread	2
<i>Myxobolus muelleri</i>	Myxobolidae	Generalist, widespread	2
<i>Myxobolus miyarii</i>	Myxobolidae	Siluridae specialist, Asia	2
<i>Sphaerospora schulmani</i>	Sphaerosporidae	³	2
Nematoda			
<i>Camallanus lacustris</i>	Camallanidae	Generalist, Eurasia	5
<i>Camallanus truncatus</i>	Camallanidae	Generalist, widespread	5
<i>Cucullanus sphaerocephalus</i>	Cucullanidae	Acipenseridae specialist, Eurasia	6
<i>Eustrongylides excisus</i>	Diectophymatidae	Generalist, Eurasia	8, 9
<i>Raphidascaaris acus</i>	Anisakidae	Generalist, Eurasia	8
<i>Schulmanella petruschewskii</i>	Capillariidae	Generalist, Eurasia	5
Platyhelminthes			
Cestoda			
<i>Bothriocephalus acheilognathi</i>	Bothriocephalidae	Generalist, widespread	5, 7
<i>Glanitaenia osculata</i> ⁵	Proteocephalidae	Specialist, Eurasia	7, 10
<i>Postgangesia inarmata</i>	Proteocephalidae	Specialist, Iraq	11
<i>Postgangesia hemispherous</i>	Proteocephalidae	Specialist, Iraq	12
<i>Silurotaenia siluri</i>	Proteocephalidae	Specialist, Eurasia	5, 9
<i>Trienophorus crassus</i>	Trienophoridae	Generalist, widespread	5
Monogenea			
<i>Thaparocleidus</i> ⁶ <i>magnus</i>	Ancyrocephalidae	Specialist, Eurasia	13
<i>Thaparocleidus siluri</i>	Ancyrocephalidae	Specialist, Eurasia	5, 7, 9
<i>Thaparocleidus vistulensis</i>	Ancyrocephalidae	Specialist, Eurasia	5, 7, 9, 14
Trematoda			
<i>Aphanurus stossichi</i>	Hemiuridae	Clupeidae specialist, Eurasia	6

Table 5 Continued.

Taxonomic groupings Parasite species	Family	Host specificity and known geographical distribution	Records for <i>S. glanis</i>
<i>Azygia lucii</i>	Azygiidae	Generalist, Eurasia	5
<i>Bunocotyle cingulata</i>	Bunocotylidae	Generalist, Eurasia	6
<i>Bucephalus polymorphus</i>	Bucephalidae	Generalist, Eurasia	5
<i>Bunodera luciopercae</i>	Allocreadiidae	Generalist, Eurasia	5
<i>Cephalogonimus retusus</i>	Cephalogonimidae	Generalist, widespread	15
<i>Cotylurus pileatus</i>	Strigeidae	Generalist, widespread	15
<i>Diplostomum spathaceum</i>	Diplostomidae	Generalist, widespread	5
<i>Metagonimus yokogawai</i>	Heterophyidae	Generalist, Eurasia	5
<i>Nicolla skrjabini</i>	Opecoelidae	Generalist, widespread	5
<i>Orientocreadium siluri</i>	Allocreadiidae	Specialist, Eurasia	5
<i>Sphaerostomum bramae</i>	Opecoelidae	Generalist, Eurasia	5
<i>Tylodelphys clavata</i>	Diplostomidae	Generalist, Eurasia	5

(1) Davronov (1987); (2) Lom and Dykova (1992); (3) Gasimagomedov and Issi (1970); (4) Dezfuli et al. (1990a); (5) Moravec (2001); (6) Mokhayer (1976); (7) Kurbanova et al. (2002); (8) Sattari et al. (2005); (9) Soylu (2005); (10) Scholz et al. (2007); (11) De Chambrier et al. (2003); (12) Rahemo and Al-Niaeeemi (2001); (13) Ondračková et al. (2004); (14) Galli et al. (2003); (15) Platyhelminths and Acanthocephala collection list (Institute of Parasitology, Academy of Sciences of the Czech Republic).

Distributions checked using authenticated on-line databases: Fauna Europea; Natural History Museum Host-Parasite Database.

¹Specialist – shows host specificity to *S. glanis* or to a specified family of fish in addition to *S. glanis*.

²Generalist – shows wide host specificity with regard to the fish host.

³The geographical distribution is not indicated in the reference and cannot be found in the published literature.

⁴*Pseudotracheilastes stellifer* is probably under-reported as it may be mis-identified as *Pseudotracheilastes stellatus* from sturgeon (Boxall, p.c.).

⁵There may be taxonomic confusion between *Glanitaenia osculata*, proposed by De Chambrier et al. (2004) to accommodate *Proteocephalus osculatus* from *S. glanis*, *P. inarmata*, *P. hemisphaerous* and *Silurotaenia siluri* (see Scholz et al. 2007).

⁶*Thaparochleidus* is the senior synonym of *Silurodiscoides* (Lim 1996) and *Ancylo-discoides* (see Moravec 2001).

probably an under-estimate because some studies, in particular those from Iran, are difficult to access. Ubiquitous fish parasites such as *Ichthyophthirius multifiliis* are not included in the list as they are present on the majority of European fish species and usually cause a health problem in cultured *S. glanis* only (Linhart et al. 2002). The diversity of parasitic fauna from *S. glanis* reflects the species' Eurasian distribution, including anthropochore from Asia to Europe (Bauer 1991) and the wide dietary spectrum of *S. glanis*, as some of these parasites are acquired through predation. There may also be evidence of host switching from sturgeons to *S. glanis*, such as *Leptorhynchoides plagicephalus*, which is considered to be specific to sturgeons (Bauer et al. 2002) but has been found in *S. glanis* from the River Pô, Italy (Dezfuli et al. 1990a).

No records of *S. glanis* mortality attributed to parasites were found in the literature, but this may be due to the aforementioned problems with detecting mortality incidents in wild fish populations. Reports of pathology associated with the listed parasites are few because of the concentration on taxonomic studies and survey data. However, fish

parasites can cause pathology when present at high intensities. For example, the Myxobolidae can have a significant pathological impact on wild and cultured fishes, and such episodes are often preceded by environmental stressors such as oxygen depletion of the water (Lom and Dykova 1992). Acanthocephalans (e.g. *L. plagicephalus*) can cause extensive damage such as lesions to the intestinal tract of fish where they attach leading secondarily to infections by bacteria (Dezfuli et al. 1990b). High intensities of parasitic crustaceans such as *Ergasilus sieboldi* can inflict severe damage to the gills (reviewed in Dezfuli et al. 2003) resulting in large scale mortalities of fish (Kabata 1979).

Reflections on the species' potential invasiveness and ecological impacts

S. glanis clearly possesses the attributes of a species well adapted to introductions outside its native range. It is an attractive species for introductions, being a popular fish for angling in many countries (Arlinghaus and Mehner 2003; Hickey and Chare 2004; Clavero and Garcia-Berthou 2006; Valadou

2007), being used for both sport and food capture. The species is also a highly appreciated culinary delicacy. *S. glanis* is sufficiently robust during transport, so permitting its translocation to areas outside its native geographical range. Once introduced, *S. glanis* appears to establish relatively easily, although the available evidence suggests that establishment is favoured in warmer climates (e.g. Mediterranean; Crivelli 1995) and may be sporadic in more northern countries (e.g. Belgium and the UK; Fraser 1979; Elvira 2001; Britton *et al.* 2007). The species' large size is suggestive of great dispersal potential, but the limited information available on *S. glanis* movements and migratory behaviour suggest that it demonstrates considerable site fidelity (Carol *et al.* 2007b), but with the potential for dispersal during hydrological events (Slavík *et al.* 2007). Equally, the most invasive fishes in Europe outside of Iberia are currently small bodied and short-lived species such as *P. parva* and the Ponto-Caspian gobies of the genera *Neogobius* and *Proteorhinus* (Copp *et al.* 2005a) as well as *L. delineatus* in the UK (Gozlan *et al.* 2003).

Although *S. glanis* is also a nest guarder, it is long-lived, rather sedentary and produces relatively fewer eggs per body mass than many fish species. Nonetheless, in a UK application of the Kolar and Lodge (2002) non-native fish profiling approach, *S. glanis* was categorized as fast spread, but non-nuisance (Gozlan and Copp, unpublished data). However, fast spread does not appear to be supported in the detailed report of Valadou (2007) on *S. glanis* in France under conditions of relatively warm water, which is already known to be suitable to the species. Having developed habitat suitability curves for *S. glanis* in France, O. Ledouble (in Valadou 2007) used logistic regression on the habitat data from 436 sites from between 1995–2004) to predict where *S. glanis* should be found. Approximately, 40% of the predicted presences (estimated from maps in Valadou 2007) were false (i.e. *S. glanis* not found), and the species occurred unexpectedly in <3% of the sites where it was predicted to be absent. No actual rate of expansion is provided, but one would expect opposite patterns, by which we mean fewer false presences and more unexpected presences, if the species were expanding rapidly. In an early study of fish movements through a fish ladder in the Czech Republic (former Czechoslovakia), only one *S. glanis* was found amongst a large number of non-salmonid fishes observed to move through the ladder (Lelek and

Libosvářský 1960). In subsequent studies using radio telemetry, the home range of *S. glanis* was found to be relatively limited, both in its native (Slavík *et al.* 2007) and introduced (Carol *et al.* 2007b) ranges, although expansion may be facilitated by man-made canal networks (Penil 2004). However, *S. glanis* seems to be quite common throughout the River Ebro (Spain), but particularly in its last 130 km from Mequinensa Reservoir (where it was introduced ca. 1974) down to the Ebro delta. Therefore, the risk of natural dispersal is likely to be slow and density dependent, but this requires detailed study.

The potential impacts of *S. glanis* in its introduced European range include disease transmission, predation on native species and possibly the modification of food web structure in some regions. However, Valadou (2007) mentions a notable impact of predation by *S. glanis* on other non-native species (*A. melas*, spiny-cheek crayfish *Orconectes limosus*). This or other species of non-native crayfish, e.g. *P. clarkii*, signal crayfish (*Pacifastacus leniusculus*, Astacidae), have invaded virtually all fresh waters of Europe (Ackefors 2000) and *S. glanis* may derive both calcium and energy from its crayfish prey (Chevalier 2004), although this requires adequate testing. There are other examples of *S. glanis* taking predominantly non-native species, such as mentioned earlier for *H. leucisculus* in the Khauzkhon Reservoir (Mukhamediyeva and Sal'nikov 1980). So, the potential relevance of this role of *S. glanis* as a 'controller' of cyprinid species, suggested by Valadou (2007) from the work of Raat (1990) and Mehner *et al.* 2001; may hold some validity. However, the role (or position) of *S. glanis* in the food webs of invaded waters remains poorly studied.

Gudger (1945) reminds us of the Bohemian proverb 'One fish is another's prey, but the sheatfish eats them all.' *S. glanis* is certainly piscivorous, but more an opportunistic forager (Mihálik 1995; Wysujack and Mehner 2005; Table 2), with human remains even being occasionally observed amongst its stomach contents (Gudger 1945). Indeed, studies of *S. glanis* in its native range have demonstrated the species to exert a relatively low (top-down) predatory pressure on zooplanktivorous fish species and the species is therefore unlikely to be an effective bio-manipulation tool in the management of lakes suffering from eutrophication (Wysujack and Mehner 2005). This would suggest that *S. glanis* is unlikely to exert competitive pressure on native

piscivorous fishes except in circumstances where other human impacts are already in force (note here that *S. glanis* is known to prey occasionally on native piscivorous species; Table 1). Furthermore, in most parts of Europe, where fish species have evolved in the presence of native piscivorous fishes (e.g. *S. lucioperca*, *E. lucius*, and Eurasian perch [*Perca fluviatilis*, Percidae]), the potential predatory impact of *S. glanis* is likely to be low (Hickley and Chare 2004). The species' greatest potential impact as a predator may be in Iberia and other southern European countries where high endemism of small-bodied fish species combines with an absence of native piscivorous fishes. However, in light of the preponderance of non-native species in the diet of *S. glanis* in artificial water bodies (Carol 2007), any such predatory impact on native species is likely to be restricted to natural river stretches. This said, recent research in Portugal indicates that the establishment and impacts of non-native fishes are facilitated in human altered water courses (i.e. reservoirs), with non-native fish species representing minor components of fish assemblages in natural, unmodified stream stretches (F. Ribeiro, personal communication).

The invasion by *S. glanis* of new areas may result in the introduction of exotic pathogens, which may or may not have already been identified. Of the recognized pathogens discussed in this review, ESV is probably the pathogen of most concern. The virus has limited distribution and its host range has not been thoroughly investigated. Its molecular similarity to other iridoviruses, such as frog virus 3 and epizootic haematopoietic necrosis (EHN), indicates that it may be capable of infecting other species of finfish or amphibians or mutation may result in jumping the species barrier. There is always a possibility that the introduction of novel fish parasites may result in deleterious consequences for the health of native fish populations (Bauer 1991). Many parasites of *S. glanis* are generalist, widespread parasites already present throughout Europe (Table 5). However, further introductions of *S. glanis* may extend the distribution of specialist species such as *Trichodina siluri*, *M. miyarui*, *L. plagiccephalus* and *Pseudotracheilastes stellifer*, the latter of which may have pathogenic potential as its congener, *P. stellatus*, is known to be pathogenic to sturgeons (Bauer *et al.* 2002).

The potential risks of *S. glanis* hybridizing with native species is likely to be limited to native *Silurus* species, such as in Greece, where the available

evidence (Paschos *et al.* 2004) suggests that *S. glanis* is able to hybridize with its congener *S. aristotelis* (Aristotle's catfish), which is listed in Annex II of the European Commission's COUNCIL DIRECTIVE 92/43/EEC (1) of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Laboratory studies have demonstrated that there is no significant variation in the survival, growth and morphology of *S. glanis* and its hybrid with *S. aristotelis*, whereas pure *S. aristotelis* exhibited low survival and variable morphology (Paschos *et al.* 2004). The hybrid demonstrated equally good survival and virtually identical morphology to *S. glanis*. It remains unknown whether the two species hybridize naturally, but it is likely given that both species have the same type of reproductive strategy, i.e. nest-guarding (Maehata 2007). Also unknown are the behaviour and other aspects of the hybrid under natural conditions.

In summary, virtually all aspects of the environmental biology of introduced *S. glanis* require study (Valadou 2007), with some initial information available on distribution (Schlumberger *et al.* 2001; Copp *et al.* 2007), movement behaviours (Carol *et al.* 2007b; Slavík *et al.* 2007), diet (Pouyet 1987; Carol 2007), diseases growth (Planche 1987a, b; Britton *et al.* 2007) and hybridization potential with native congeners (Paschos *et al.* 2004). However, the existing evidence does not suggest that *S. glanis* is a voracious predator, but rather an opportunistic scavenger, and as such it does not appear to present a particularly great threat where introduced. In an initial invasive-ness assessment (Copp *et al.* 2005b), *S. glanis* attracted an intermediate mean risk score (21.5 of 54 possible points), which places it in the lower part of the 'high risk' score range (Copp *et al.* (in press); 19–54. And the lack of evidence for demonstrated impacts (e.g. low predation on native fishes in Iberia; Carol 2007) would appear to corroborate this assessment. This emphasizes that caution may be advised when assumptions of adverse impact (Rodríguez-Labajos 2006) are based on anecdotal information sources (i.e. Doadrio 2001; Carol Bruguera 2004).

As with *L. delineatus* (Gozlan *et al.* 2003), *S. glanis* has perhaps the unusual distinction of being a species threatened in its native range (Nathanson 1987; Shilin 1987; Saat 2003), where it is also successfully cultured (Adámek *et al.* 1999; Ulikowski 2004), and at the same time a successfully introduced species elsewhere in Europe, if not other continents (Ma *et al.* 2003). Unusually, *S. glanis*

may even be threatened by a conspecific (*S. aristotelis*) within Greece, where the two species are native to different parts of the country (Economidis *et al.* 2000). Therefore, the most urgent need for research on *S. glanis* is to assess the species' potential impact (or not) on aquatic food webs (Wysujack and Mehner 2005), especially in riverine ecosystems. One means of delving deeper into the ontogenetic shifts of feeding patterns and prey selection in *S. glanis* is stable isotope analyses, which are a temporally integrative tool to analyse longer-term dietary records. Indeed, stable isotope analysis has already provided a means of assessing the ecological impacts of non-native species on other aquatic food webs (Vander Zanden *et al.* 1999; Cucherousset *et al.* 2007), and its use in the introduced range of *S. glanis* is expected to be particularly informative.

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